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By W. Stephenson, W. T. Williams, and G. N. Lance[1]

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This paper attempts an assessment of the status and interrelationships of various taxa of American portunids within the genera *Portunus*

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Weber 1795, *Callinectes* Stimpson 1860, and *Arenaeus* Dana 1851 by other than the classical techniques of descriptive systematics.

The work began by detailed comparisons between pairs of species in each of the genera. Rathbun (1930) has listed eight pairs of analogous species (or twin species, or geminate species) in which one of each pair is a western American species and one an eastern. Most of these are not clearly detectable by a classical approach (Garth and Stephenson, 1966), which instead has suggested "confused" relationships between groups of western and groups of eastern species. Nine of the ten western "species" (including one subspecies; authors and dates of species are given in table 1) of *Portunus* appear closely related. Several different dichotomous keys can be devised for their separation, but none has obvious precedence for convenience or indications of relationships. (The key to the western species that eventually was adopted employed an initial pentachotomy.) It seemed that all characters had equivalent hierarchial significance. The problems of establishing a hierarchy are emphasised by the fact that Rathbun (1930) had used two subgenera, *Portunus* and *Achelous* de Haan 1833, that are linked by continuous variation within one species, *P. xantusii*.

To some extent the present work was a trial of numerical techniques and initially involved a small number of species, the nine western species of *Portunus*. When the eastern species of the genus were added, the increased complexity of information gave added convenience to the numerical methods.

As the work progressed, it was widened to include the relationships among *Callinectes*, *Arenaeus* (which is very close to it; see Garth and Stephenson, 1966, p. 52), and *Portunus*. *Callinectes* is a particularly interesting case. Stephenson and Campbell (1959, p. 88) questioned whether *Callinectes* differs sufficiently from the general span of the genus *Portunus* for it "to have more than the status of a subgenus if such are to be recognised."

When *Callinectes* species are compared with western American *Portunus* species, there are numerous differences. Garth and Stephenson (1966), partly influenced by preliminary results of the present work, retained *Callinectes* as a genus. It is diagnosed by three features only (Garth and Stephenson, 1966, p. 42): (1) male abdomen ⊥-shaped, which is shared with certain Indo-West Pacific species of *Portunus* and with *Arenaeus;* (2) anteroexternal angle of merus of third maxilliped strongly produced outward, which is shared with many species of *Portunus;* (3) wrist of cheliped without an inner spine, which is the only unique feature.

When eastern American *Portunus* species are considered, the morphological gap to *Callinectes* becomes partly bridged. If the

type-species of the genus *Portunus*, *P. pelagicus*, is considered, a general classical impression is gained that *Callinectes* species are closer to *P. pelagicus* than are the bulk of the American species of *Portunus*. Inclusion of *P. pelagicus* suggested to us that additional Indo-West Pacific species should be considered, involving several species close to *P. pelagicus*, *P. macrophthalmus* for comparison with *P. tuberculatus*, and *Scylla serrata* exemplifying another related genus.

The number of species eventually compared (44) is sufficiently large to give convenience to numerical techniques but not too large for the conclusions from each technique to be checked against the "common sense" of the classical background. With such comparison possible, we found it not surprising that the overall outlook on the group has not been changed materially. The important conclusions, therefore, are in the field of methodology. It was hoped that a method would be developed that could be applied to the very numerous Indo-West Pacific species of *Portunus*, whose complex interrelationships are difficult to determine by the traditional approach.

Numerical Methods

FORM OF DATA.—Basic taxonomic data normally are mixed: they may, for example, comprise attributes that are qualitative ("yes" or "no", "present" or "absent"), multistate (A, B, or C), ordered multistate or ranked ("absent", "rare", "common"), and numerical (measured). Few numerical models capable of accommodating all these approaches are known; and, although computer programs using such models exist, they are relatively inflexible and allow little or no choice of alternative approaches in an exploratory situation. There are, therefore, advantages in using simpler types of data if this is practicable within the problem under study. When very closely-related organisms are concerned—for example, in intraspecific comparisons—the investigation normally involves measured characters, and these alone may suffice. Interspecific comparisons usually involve qualitative differences, and it may be advantageous to reduce all the data to the qualitative form. The advantages are: first, data can be tabulated in an extremely economical form, which permits rapid intuitive assessment of taxonomic similarities; and second, numerical systems for processing qualitative data are powerful, fast, and flexible, and their properties are well understood.

Certain problems, nevertheless, remain to be resolved: (1) decision must be taken as to whether double-negative matches are to count as evidence of similarity (past experience of numerical classifications suggests that they should do so, and the programs at our disposal all make this assumption). (2) Provision must be

made for missing or inapplicable attributes (the latter arise if, as is commonly the case, the applicability of later questions depends on the answer to earlier ones). (3) The dichotomizing of a single multistate attribute always generates a set (at least two) of qualitative attributes, and these are linked logically in the sense that certain combinations of states will be redundant (experience suggests that this will not disturb the analysis, provided the number of originally multistate attributes is small; Watson, Williams, and Lance, 1966). (4) In a completely qualitative system no provision can be made for "doubtful" entries (in the present case these comprised less than 2 percent of the total). (5) A character may be capable of subdivision; for example, carapace ornamentation can be reduced to the single character "mostly ridges present rather than raised granular areas," or (as in the present case) the ridges can be listed separately; this decision necessarily involves the concept of "weighting" and must be resolved on taxonomic grounds, not numerical grounds.

As the investigation proceeded, 44 species eventually were compared by reference to 57 features (selected features are listed in table 1, species in table 2, and data in table 3).[2] Selected features were those believed likely to give good overall discrimination. Had particular comparison been an issue, other characters might well have been more appropriate. The wording of the features was designed to give positive answers to our specific questions for most of the western American *Portunus* species.

During tabulation of data, the inadequacy of many past descriptions of the species became apparent. Such descriptions have concentrated upon specific recognition and distinctions from nearly related species but have omitted similarities to more distant species.

NUMERICAL MODEL.—Any study of inter-relationships requires the definition of a measure of likeness to serve as the basic numerical model of the system. Such measures—the so-called "similarity coefficients"—have been proposed in great variety; the best known are summarized and defined in Goodman and Kruskal (1954, 1959), Dagnelie (1960), and Sokal and Sneath (1963). The simplest measure of difference between two qualitatively specified individuals is the "number of features of difference" (the NFD value) wherein one individual scores + and the other −. In the conventional "*a*, *b*, *c*, *d*" symbolism of a 2×2 contingency table, this is the quantity "*b*+*c*." Moreover, if we regard the attributes as defining a set of orthogonal axes in Euclidean space and regard the coordinate along a given axis as "1" (if the feature is possessed) and "0" (if it is lacking), "*b*+*c*" then represents the square of the Euclidean distance between the two

[2] Tables at end of paper.

individuals concerned. Alternatively, the square root of this quantity (i.e., the Euclidean distance itself) may be used as a measure of "taxonomic distance" (TD). Preliminary investigations using other measures—the correlation coefficient, the nonmetric coefficient, and Euclidean distance standardized to zero mean and unit variance—suggested that these offered no advantages over the NFD and TD values. The latter, therefore, have been used throughout this study.

STRATEGY.—In the present problem we were concerned not only with the overall configuration of inter-relationships but also with the possible light that this might throw on certain specified problems. We used three approaches:

(1) Direct comparison of intergroup NFD and TD values: Since the original values relate only to distances between individuals, a further definition of individual/group or group/group distance is required. The distance between group centroids commonly is used for this purpose, but this is troublesome to calculate from the inter-individual NFD or TD values and requires manipulation of the original data. We, therefore, have preferred to use the "group-average" measure of Sokal and Michener (1958), whereby the distance between two groups is defined as the average of all interindividual between-group NFD or TD values.

(2) Classification: General accounts of classificatory methods are given in Sokal and Sneath (1963), MacNaughton-Smith (1965), and Williams and Dale (1965). Four methods were used: (a) nearest and farthest neighbor sorting of the NFD values; (b) centroid sorting using the original data; (c) the nonmetric coefficient; and (d) information analysis (Williams, Lambert, and Lance, 1966). The results were disappointing: groups were not clear-cut, and the configurations obtained by various methods differed considerably. Although it would now be possible to increase the clarity of the picture by the greater power of "flexible" sorting (Lance and Williams, 1967), the process is not to be recommended in the current situation. The variability of the results suggests that at least part of the system is more or less continuous, with the result that ordination, rather than classification, is likely to represent the most fruitful approach. The classificatory approach, therefore, was abandoned, and the results are not presented in this paper.

(3) The efficient representation of a multidimensional system in fewer dimensions normally would be undertaken by principal component analysis. In our case, however, several attributes are missing from one of the individuals, a fact that would complicate the calculation. It is desirable, therefore, to ordinate the interindividual matrix of mean NFD values. This problem is discussed in Sokal and Sneath (1963), but the methods given therein are empirical, since at that

time no general solution to the problem was known. The transformation established by Gower (1966) now provides a simple and elegant solution. We write d_{ij} for the average NFD value between individuals i and j; we form a matrix (a_{ij}) such that $a_{11}=a_{jj}=0$ and $a_{ij}=-\frac{1}{2}(d_{ij})^2$. Let the row-means of this matrix be the vector $(a_{i.})$, the columns means $(a_{.j})$, and the grand mean $a_{..}$; we then form the matrix (b_{ij}), where $b_{ij}=a_{ij}-a_{i.}-a_{.j}+a_{..}1$. The eigenvalues and eigenvectors of this matrix are extracted and standardized so that the length of each vector is equal to the value of its corresponding root. Gower demonstrates that these vectors define a Euclidean space in such a way that the distance between two individuals is equal to its original d_{ij} value, and in such a way that the space has been reduced as efficiently as is possible with a linear transformation. (The space is not everywhere real, but this is of no importance in practice.) In our case, three axes were found to suffice for the general configuration, but any substantial deviations in the next three axes were noted.

It is possible to simplify the configuration further by moving overtly into the techniques of factor analysis. Given that three axes are all that is required, the requirement is to reduce the values of the principal diagonal of the "b_{ij}" matrix so that the least possible information remains in the matrix after the extraction of three positive roots. The method is explained in standard books on factor analysis (e.g., Cattell, 1952; Thomson, 1951); it is iterative and somewhat time-consuming in computation. Automatic programs exist on the Control Data Corporation 3600 computer at Canberra for the basic ordination (program GOWER) and the factor-analysis version (NEWGOWER). These two programs accept the upper triangle of the original (d_{ij}) matrix as a string of coefficients and carry out all subsequent adjustments and calculations automatically.

Material Examined

All known American species of *Portunus*, *Callinectes*,[3] and *Arenaeus* were examined. Also examined were: (1) certain Indo-West Pacific species of *Portunus*, comprising *P. pelagicus*, *P. sanguinolentus*, *P. pubescens*, *P. convexus*, and *P.* cf. *tuberculatus;* (2) the known non-American species of *Callinectes;* and (3) *Scylla serrata* for comparison with the distinctness of other genera.

The species examined are listed in table 2. Extensive series of western American forms were examined, as recorded in Garth and Stephenson (1966), but fewer specimens of Atlantic species were seen, and there were no critical examinations of difficult groups. Atlantic species were

[3] Since this paper has been completed, Williams (1966) has described a new species of *Callinectes*, *C. similis*, which is commented upon later (p. 18)

identified from type-material or from specimens identified by Rathbun. Most Indo-West Pacific species were known from previous investigations (Stephenson and Campbell, 1959; 1960) or from types; however, one was based upon a recently collected Australian specimen related, but not identical with, *P. trituberculatus*. (Further study showed this to be an unusual specimen of *P. pelagicus*, which differs in only a single tabulated feature from *P. trituberculatus:* it lacks the tubercles on the carapace: feature *13* in table 1). Another Indo-West Pacific species, *P. convexus*, was based upon the literature, mostly from Crosnier (1962).

To simplify later treatment, all species and subspecies are referred to in the text below as "species." Throughout the text, ringed numbers that accompany specific names are those listed in table 2.

Results

Our investigation considered, first, certain specific questions relevant to the taxonomic problem and, second, the larger scale inter-relationships and the evidence they provide for parallel evolution. Conclusions were based, first, on inspection of the NFD and TD values obtained from the tabular data of table 3, and, second, on the 3-dimensional ordination of the numerical models. Since 2-dimensional sections proved somewhat unrevealing, 3-dimensional models were constructed. Figures 1 and 2 have been drawn from oblique photographs of the model obtained from the basic GOWER ordination. Several of the plotted points in this model may be regarded as spuriously close together since substantial deviations in the fourth, fifth, and sixth axes are suppressed. Each instance of a deviation greater than 100 scale units is shown by a black spot in the figures; a considerable number of such discrepancies is evident. Figures 3 and 4 have been derived from similar photographs of the model obtained from the NEWGOWER ordination, which had been reduced by iteration to three factor axes.

Specific Questions

ANALOGOUS SPECIES.—Consideration of both tabular data and the models indicated that none of the following pairs of species of *Portunus* listed as analogous by Rathbun (1930) can be considered analogous (pairs are listed with western species first): *P. xantusii xantusii* ⑧/ *P. gibbesii* ⑮; *P. brevimanus* ④/*P. spinimanus* ㉑; *P. angustus* ②/ *P. ordwayi* ⑯; and *P. iridescens* ⑥/ *P. spinicarpus* ⑳.

While the general conclusions from the two methods are identical, the models distort some of the detailed relationships of the above species to other species; for example, in the models, *P. iridescens* ⑥

appears closer to *P. stanfordi* ⑦ and *P. acuminatus* ① than to *P. spinicarpus* ㉙ and *P. guaymasensis* ⑤, which are its nearest neighbors on both tabular and classical grounds.

Neither of the following pairs of species of *Callinectes* can be con-

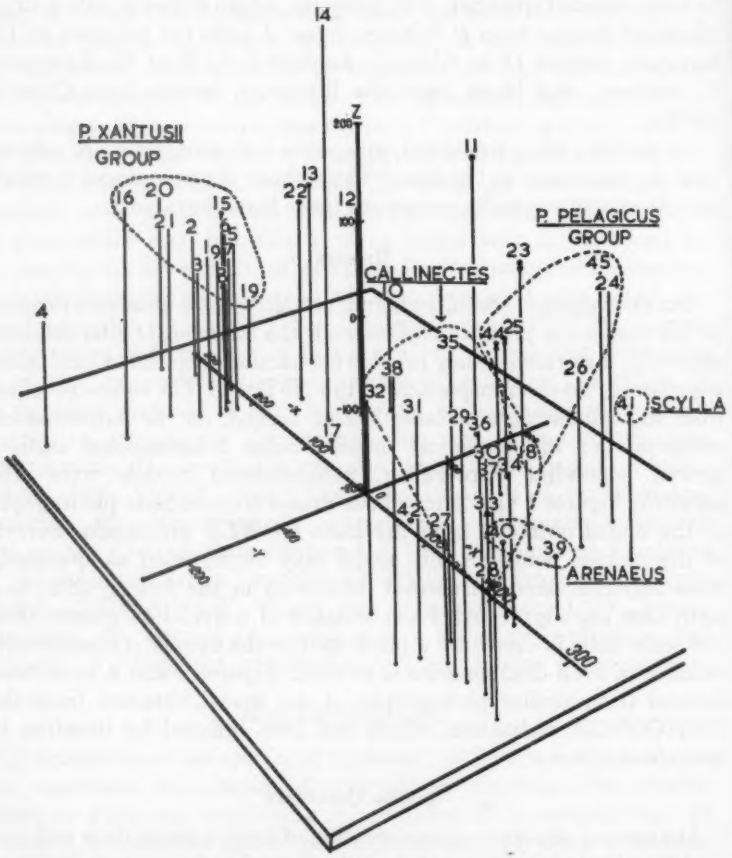

FIGURE 1.—Model from basic GOWER ordination based on an oblique photograph taken from the "southeast" (black spots = deviations greater than 100 scale units in the fourth, fifth, and sixth axes; dotted lines = species groups).

sidered analogous from tabular data or from model inspection: *C. bellicosus* ㉙/*C. sapidus acutidens* ㉗ and *C. toxotes* ㉘/*C. boucourti* ㉙. From consideration of tabular data, *C. arcuatus* ㉗ and *C. danae* ㉚ are an analogous pair (NFD 3). This is not apparent from the model

first figured (figs. 1 and 2) but it is indicated in the second (figs. 3 and 4).

Arenaeus mexicanus ㊵/*A. cribrarius* ㊴ as the only two species in the genus presumably must be analogous although there are numerous

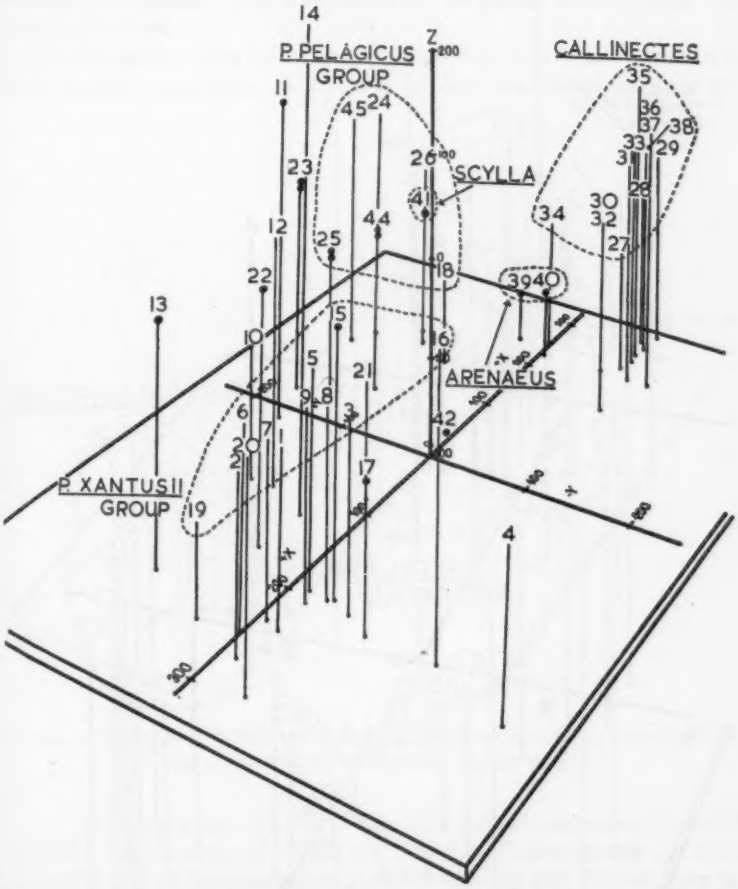

FIGURE 2.—Model from basic GOWER ordination based on an oblique photograph taken from the "southwest" (black spots = deviations greater than 100 scale units in the fourth, fifth, and sixth axes; dotted lines = species groups).

differences in tabular data (NFD 7) and they are some distance apart on the models.

Evidently, at most, one of the postulated pairs of analogous species has clear claims to such a status. We believe it is desirable that

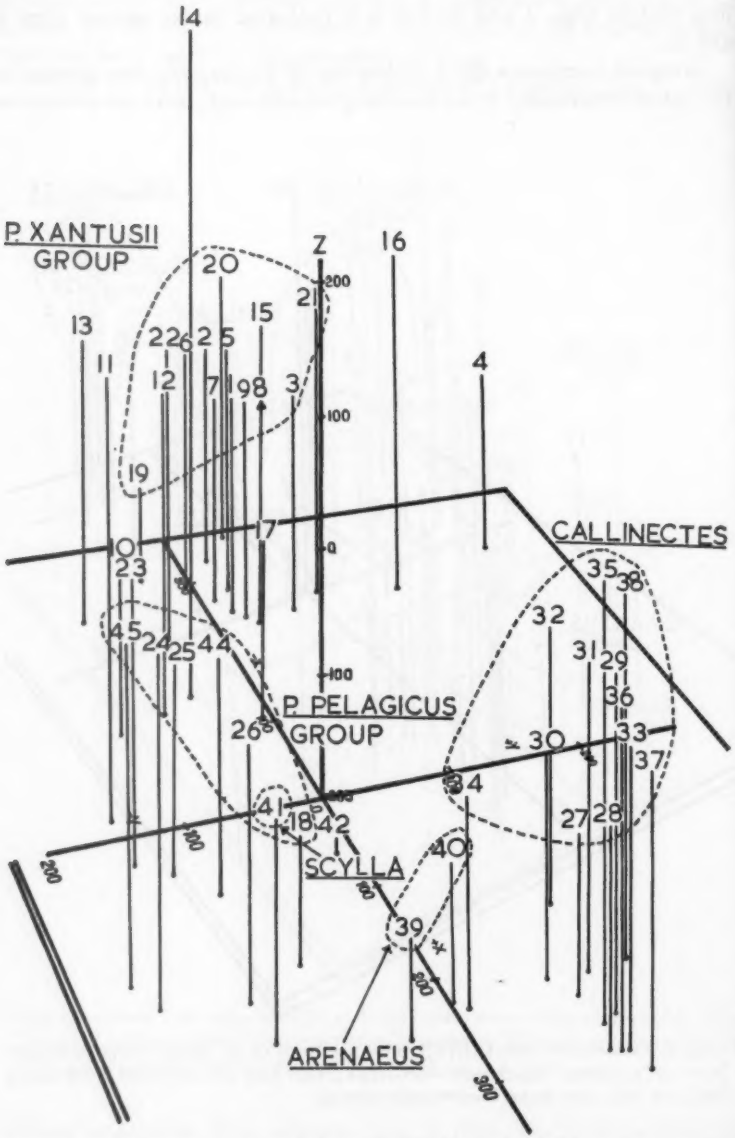

FIGURE 3.—Model from NEWGOWER ordination based on an oblique photograph taken from the "southeast" (dotted lines = species groups).

examples of analogous pairs in other crustacean groups should be re-investigated.

RELATIONSHIPS AMONG WESTERN AMERICAN GROUPS OF *PORTUNUS*.—These comprise species ①–⑩, inclusive, of table 2. Consideration of NFD or TD values or inspection of the models shows that *P. tuberculatus* ⑩ is distant from the remainder, as known already from the classical studies.

Tabular data: The remaining nine species give mean values (of each species considered in relation to the remainder) as follows:

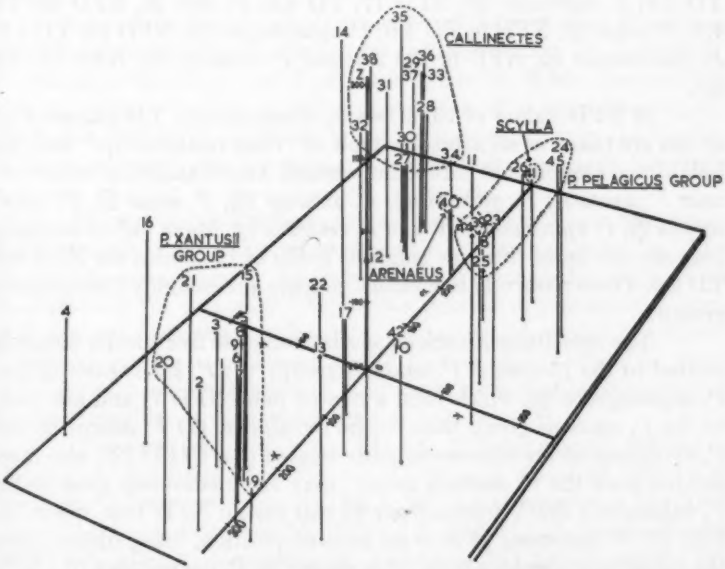

FIGURE 4.—Model from NEWGOWER ordination based on an oblique photograph taken from the "southwest" (dotted lines=species groups).

P. acuminatus ①, NFD 6.3, TD 2.3; *P. angustus* ②, NFD 7.6, TD 2.7; *P. asper* ③, NFD 6.1, TD 2.4; *P. brevimanus* ④, NFD 11.0, TD 3.3; *P. guaymasensis* ⑤, NFD 8.0, TD 2.8; *P. iridescens* ⑥, NFD 8.8, TD 2.8; *P. stanfordi* ⑦, NFD 7.3, TD 2.7; *P. xantusii xantusii* ⑧, NFD 5.4, TD 2.2; and *P. xantusii affinis* ⑨, NFD 5.6, TD 2.3.

These data suggest that *P. xantusii* with its two subspecies ⑧ and ⑨ and also *P. acuminatus* ① are close to the "morphological center" of the western American species of *Portunus*.

Inspection of the models: These show that the above nine species are grouped closely with the possible exception of *P. brevimanus* ④.

The models also show an "incenter" of the above species approximately midway between *P. xantusii xantusii* ⑧ and *P. acuminatus* ①.

RELATIONSHIPS OF THE REMAINING AMERICAN SPECIES OF *PORTUNUS* TO THE WESTERN GROUP OF NINE.—These comprise species ⑩–㉒ and also ㊷ of table 2.

Tabular data: Mean values of eastern species to both *P. xantusii xantusii* ⑧ and *P. xantusii affinis* ⑨ were computed and are as follows: *P. anceps* ⑪, NFD 20, TD 4.5; *P. bahamensis* ⑫, NFD 16, TD 4.1; *P. depressifrons* ⑬, NFD 16, TD 3.7; *P. floridanus* ⑭, NFD 17, TD 4.2; *P. gibbesii* ⑮, NFD 10, TD 3.0; *P. ordwayi* ⑯, NFD 7, TD 2.8; *P. rufiremus* ⑰, NFD 17, TD 4.0; *P. sayi* ⑱, NFD 24, TD 4.8; *P. sebae* ⑲, NFD 9, TD 3.0; *P. spinicarpus* ⑳, NFD 10, TD 3.2; *P. spinimanus* ㉑, NFD 6, TD 2.6; and *P. ventralis* ㉒, NFD 10, TD 3.0.

If NFD values of 10 or less or, alternatively, TD values of 3.3 or less are taken as an arbitrary limit of "close relationship," then the following six species are part of the western American group "centered" near *P. xantusii*: *P. gibbesii* ⑮, *P. ordwayi* ⑯, *P. sebae* ⑲, *P. spinicarpus* ⑳, *P. spinimanus* ㉑, and *P. ventralis* ㉒. Mean values mutually between species of this now enlarged group of 15 species are NFD 9.6, TD 3.0. These relatively low values indicate a reasonably homogeneous group.

The remaining American species comprise five species distantly related to the 15-species *P. xantusii* group: (1) *P. bahamensis* ⑫ and *P. depressifrons* ⑬, which form a related pair (NFD 7) and are closer to the *P. xantusii* group than to the remainder. (2) *P. anceps* ⑪ and *P. floridanus* ⑭ are a more distantly related pair (NFD 12), also more distant from the *P. xantusii* group; they are moderately close to the *P. bahamensis* ⑫/*P. depressifrons* ⑬ pair (mean NFD 16.3, mean TD 4.0). (3) *P. rufiremus* ⑰ is in an isolated position, being distant from the other four species above; it is closest to *P. acuminatus* ① (NFD 13). (4) The western American *P. tuberculatus* ⑩ is related to the Indo-West Pacific species in the *P. longispinosus* group (see Garth and Stephenson, 1966; Stephenson and Rees, 1967); because of synonymy problems within this group, *P. tuberculatus* ⑩ was compared with the only "fixed point" available, the holotype of *P. macrophthalmus* ㉓; it is closer to this species (NFD 11) than to the nearest member of of the 15-species group (NFD 13 to *P. x. xantusii* ⑧); it is probably closer to other species in the *P. longispinosus* group, and shows a distant relationship to *P. vocans* ㊷ (see following). (5) The eastern *P. vocans* ㊷ is so similar to *P. nipponensis* (Sakai) 1938 from Japan that numerical techniques are unnecessary; it probably is related distantly to *P. tuberculatus* ⑩, *P. macrophthalmus* ㉓, and other members of the *P. longispinosus* group, but since only a female was

available for study, full tabular data could not be obtained; *P. vocans* ㊷ is not restricted to American waters, occurring also at Ascension Island in the South Atlantic (Rathbun, 1930). (6) The eastern *P. sayi* ⑱ is a member of the *P. pelagicus* group (see p. 15).

Inspection of the models: From the models, the same eastern species are part of the *P. xantusii* group: *P. gibbesii* ⑮, *P. ordwayi* ⑯, *P. sebae* ⑲, *P. spinicarpus* ⑳, *P. spinimanus* ㉑, and *P. ventralis* ㉒; however, *P. ventralis* ㉒, which was a borderline case from the tabular data, now becomes an even more doubtful member of the group.

Again from the models, the incenter of the 15-species *P. xantusii* group is approximately equidistant from *P. acuminatus* ①, *P. asper* ③, *P. xantusii xantusii* ⑧, and *P. xantusii affinis* ⑨. While the term "*P. xantusii* group" implies an oversimplification, it is considered significant that all four of the above "central" species occur in the Pacific. It seems probable that the group originated from a western American ancestor.

The remaining American species (apart from *P. sayi* ⑱) appear in the models to be scattered between the *P. xantusii* group and the *P. pelagicus* group (see p. 15), apart from *P. depressifrons* ⑬, which is somewhat "to one side." While the general arrangement follows that derived from the tabular data, no pairing of species is evident.

RELATIONSHIPS AMONG SPECIES OF *CALLINECTES*.—Tabular data: Consideration of the species of *Callinectes*, each mutually in relation to the remainder, gives mean values as follows:

C. arcuatus ㉗, NFD 6.8, TD 2.6; *C. bellicosus* ㉘, NFD 9.0, TD 3.0; *C. boucourti* ㉙, NFD 5.5, TD 2.3; *C. danae* ㉚, NFD 5.8, TD 2.5; *C. exasperatus* ㉛, NFD 6.8, TD 2.6; *C. gladiator* ㉜, NFD 7.4, TD 2.7; *C. latimanus* ㉝, NFD 4.9, TD 2.1; *C. marginatus* ㉞, NFD 8.9, TD 3.0; *C. ornatus* ㉟, NFD 6.0, TD 2.4; *C. sapidus* ㊱, NFD 5.4, TD 2.3; *C. sapidus acutidens* ㊲, NFD 5.5, TD 2.2; *C. toxotes* ㊳, NFD 5.2, TD 2.2. The mean overall values of NFD 7.2 and TD 2.5 indicate that the genus is very homogeneous.

The west African species *C. latimanus* ㉝ is closest to the "morphological center" in this predominantly Atlantic genus. The three western American species differ appreciably from each other, with *C. toxotes* ㊳ closest to the bulk of the remaining species and particularly close to five Atlantic species (*C. boucourti* ㉙, *C. ornatus* ㉟, *C. sapidus acutidens* ㊲, and *C. latimanus* ㉝, all NFD 3; and *C. exasperatus* ㉛, NFD 4). On structural and distributional grounds any of the first three could have given rise to *C. toxotes* ㊳ as a result of a Pacific isolate. The second Pacific species, *C. bellicosus* ㉘, forms an analogous pair with *C. danae* ㉚, and presumably they had a common origin.

Inspection of the models: The models show the genus as a close-packed group. In the first figured model (figs. 1 and 2) *C. gladiator* ㉜ and *C. marginatus* ㉞ are the most peripheral species. This differs somewhat from the results of the tabular data, in which *C. bellicosus* ㉘ and *C. marginatus* ㉞ were the most peripheral species. The second figured model gives a closer approximation to the tabular data, with *C. marginatus* ㉞ as a peripheral species. The "incenter" in the first figured model lies approximately equidistant from *C. boucourti* ㉙, *C. danae* ㉚, and *C. ornatus* ㉟; in the second model, the "incenter" lies approximately midway between *C. arcuatus* ㉗, *C. bellicosus* ㉘, and *C. boucourti* ㉙. These results differ from the tabular consideration, in which *C. latimanus* ㉝ was the "focal" species. It is considered significant that most of the postulated "central" species occur in the Atlantic, and it is conceivable that the group originated from an eastern American ancestor. It seems virtually certain that the western American forms arose from eastern American ancestors.

Portunus pelagicus ㉔ and related species of *Portunus*.—Five species are known on classical grounds to be related closely, forming a *P. pelagicus* "group": *P. pelagicus* ㉔, *P. sanguinolentus* ㉖, *P. pubescens* ㉕, *P. convexus* ㊹, and *P. trituberculatus* ㊺.

Neptunus madagascariensis Hoffman, 1874, has not been included in this group in spite of its obvious resemblance to *P. sanguinolentus* ㉖, which has been commented upon by both Hoffman (1874, p. 8) and Crosnier (1962, p. 47). Crosnier put the species in the genus *Portunus*. Hoffman, however, stated in his description that it differed from *Neptunus diacanthus* Latreille, 1825, only in "l'absence de l'épine sur le bord posterieur du bras. Cette différence est tellement minime que cette espèce ne forme peut-etre qu'une variété de *Neptunus diacanthus*." The varieties of *N. diacanthus* of Hoffman's time are now species of *Callinectes*, and Miers (1886) has suggested already that *N. madagascariensis* belongs to *Callinectes*. It possesses the following diagnostic features of that genus: anteroexternal angle of merus of third maxillipeds expanded and wrist of cheliped without inner spine. The absence of a spine on the posterior border of the arm is shared with *C. exasperatus* ㉛ although the species keys out from Rathbun (1930) as *C. danae* ㉚. It is unfortunate that this most interesting species is known only from the holotype female, whose present location is unknown.

Stephenson (1968, in press) recently has obtained evidence of the existence of an undescribed subspecies of *P. sanguinolentus* ㉙. This has been omitted from present consideration because it is identical with normal *P. sanguinolentus* ㉖ on the basis of the list of features that are used herein.

Consideration of the results in table 3 and of the models showed that *P. sayi* ⑱ clearly belongs to the *P. pelagicus* group; thus, six species in the group were considered.

Tabular data: Mean values of each species considered separately against the remainder are as follows:

P. sayi ⑱, NFD 13.0, TD 3.6; *P. pelagicus* ㉔, NFD 9.2, TD 3.0; *P. pubescens* ㉕, NFD 12.8, TD 3.5; *sanguinolentus* ㉘, NFD 11.6, TD 3.4; *P. convexus* ㊹, NFD 11.0, TD 3.3; and *P.* cf. *trituberculatus* ㊺, NFD 11.1, TD 3.2. The overall means of NFD 11.5 and TD 3.3 indicate a less homogeneous group than either the *P. xantusii* group or the genus *Callinectes*. No individual species is close to the "morphological center."

Inspection of the models: Identical conclusions were obtained.

General Considerations

INTERGROUP AND INTERGENERIC RELATIONSHIPS.—The critical group is probably the six species in the *P. pelagicus* group, and this has been considered in relation to the remainder.

Tabular data: Mean values to other groups are as follows:

(1) *P. xantusii* group (15 species), NFD 26.6, TD 5.2. The species in the *P. pelagicus* group closest to the *P. xantusii* group is *P. convexus* ㊹, NFD 23.9, TD 4.9. The species in the *P. xantusii* group closest to the *P. pelagicus* group is *P. ventralis* ㉒, NFD 22.8, TD 4.8, closely followed by *P. xantusii xantusii* ⑧, NFD 23.7, TD 4.9.

(2) *Callinectes* species (12), NFD 17.4, TD 4.2. The species in the *P. pelagicus* group closest to *Callinectes* species is *P. sanguinolentus* ㉘, NFD 14.5, TD 3.8. The species of *Callinectes* closest to the *P. pelagicus* group is *C. marginatus* ㉞, NFD 15.2, TD 3.9.

(3) *Arenaeus* species (2), NFD 17.0, TD 4.1. The species of *Arenaeus* closest to the *P. pelagicus* group is *A. cribrarius* ㊴, NFD 16.3 TD 4.0. The species of the *P. pelagicus* group closest to *Arenaeus* species is *P. sayi* ⑱, NFD 11.5, TD 3.4.

(4) *Scylla* species (1), NFD 20.3, TD 4.5. The species of the *P. pelagicus* group closest to *Scylla* is again *P. sayi* ⑱, NFD 16, TD 4.

These values show: (1) The *P. pelagicus* group is much further from the bulk of the American species of *Portunus* (the *P. xantusii* group) than it is from *Callinectes*, *Arenaeus*, or *Scylla*. (2) The degree of separation of *Arenaeus*, plus *Callinectes*, from the *P. pelagicus* group is greater than the average separations between the members of this group; hence, the genus *Portunus* stands apart from these two genera. (3) *Scylla* is even more distant from the *P. pelagicus* group. (4) The most doubtful of the classical separations is that between *Arenaeus* and *Callinectes*. While *Callinectes* species form a homogeneous entity

(mean NFD 7.2, TD 2.5), the two species of *Arenaeus* scarcely can be excluded from this assemblage; thus, *A. cribrarius* ㊴ is closer to *C. bellicosus* ㉘ (NFD 11) than this species is to *C. exasperatus* ㉛, *C. gladiator* ㉜, and *C. marginatus* ⑭. It would seem desirable to re-examine these genera in the first instance by a detailed classical approach. (5) The genus *Portunus* covers a wide range of morphological diversity. If only the *P. pelagicus* group and the *P. xantusii* group are considered, clearly these should belong to different genera.

Inspection of the models: On the one hand, this confirmed visually the main conclusions (1), (2), (4), and (5) above; on the other hand, the validity of separating *Scylla* from the *P. pelagicus* group appears very doubtful. In addition, the detailed relationships of individual species are altered; for example, *P. sayi* ⑱ becomes the closest species of the *P. pelagicus* group to *Callinectes*; also the closest approach of *Arenaeus* and *Callinectes* species are *A. mexicanus* ㊵ and *C. marginatus* ㉞.

EVIDENCES OF PARALLEL EVOLUTION WITHIN THE GENUS *PORTUNUS*.—The following main groups have been recognized in the above discussion: (1) 15 species group centered on *P. xantusii*; (2) *P. pelagicus* group; (3) *P. longispinosus* group, represented in America by *P. tuberculatus* ⑩; (4) *P. vocans* group, containing a second species from the Indo-West Pacific; (5) an indistinct *P. bahamensis* group, containing *P. bahamensis* ⑫, *P. depressifrons* ⑬, *P. anceps* ⑪, and *P. floridanus* ⑭.

In many cases a given taxonomic feature occurs in species belonging to two or more of the above groups. In a few cases it occurs in only some of the species of the groups, in which case presumably parallel evolution has occurred. Excluding secondary sexual characters of the males, the features showing parallel evolution are as follows (feature numbers are from table 1, unnecessary negatives having been eliminated):

2 Median frontal lobes forming pointed teeth.
6 Inner supraorbital sinus open.
7 Third maxilliped not conspicuously hairy.
11 Carapace not hairy.
12 Carapace broad.
14 Postlateral junction of carapace spinous.
16 Mesogastric area of carapace with broad granular ridge.
26 First anterolateral tooth more slender than second.
28 Last anterolateral tooth distinctly long.
29 Chelae attenuated.
30 Chelae robust.
31 Undersurface of chelae with squamiform markings.
33 Posterior border of arm without spines.
37 Hand of chelae swollen.
39 Upper surface of hand with single spine.
40 Posterodistal border of merus of fifth leg spinulose.
57 Iridescence present somewhere on body.

An additional feature is the presence of large red spots on the posterior portion of the carapace.

Many of these are without great evolutionary significance and do not appear early in keys. Others do (e.g., *14*, *29*, and *33*) and even have been used for subgeneric distinctions (e.g., *14*). Knowledge of the characters of a wide range of Indo-West Pacific species (Stephenson and Campbell, 1959; Stephenson and Rees, 1967) suggests that many additional features result from parallel evolution (e.g., expansion of the antero-external angle of the merus of the third maxilliped).

The problems of recognising subgenera of *Portunus* by classical criteria have been detailed (Stephenson and Campbell, 1959). The present study, by showing gradations in affinities among several groups or complexes and by adding to the list of features showing parallel evolution, does not make this recognition any easier.

General Conclusions

With the work carried out against a background of classical knowledge of the group, we found it not surprising that most of the detailed conclusions do not greatly distort the accepted patterns. The most significant of these conclusions appear to be as follows:

(1) Analogous pairs of species of portunids with Pacific and Atlantic forms are far from recognisable in most cases.

(2) There are about 15 closely related American species, herein called the *P. xantusii* group, which comprise nine Pacific and six Atlantic species. This group appears to have originated from Pacific ancestors.

(3) The genus *Callinectes* appears to have had an Atlantic origin.

(4) One primarily Atlantic species, *P. sayi* (18), belongs to the predominantly Indo-West Pacific *P. pelagicus* group. *P. sayi* is possibly the species in the group most closely related to the genera *Arenaeus* and *Callinectes*.

(5) There are grave doubts over the validity of separating *Arenaeus* from *Callinectes*; these genera merit monographic treatment.

Possibly the most important conclusions concern methodology. In working on the American forms of *Portunus*, *Callinectes*, and *Arenaeus* we hoped to develop techniques that could be applied to the very numerous Indo-West Pacific species of *Portunus*, whose complex interrelationships are difficult to clarify by the traditional approach.

The results have shown that (1) for the recognition of groups, the method embodied in the 3-dimensional models is entirely acceptable; of these models, the second (based on three axes only) appears slightly preferable; (2) for the detailed consideration of affinities within the groups, the tabular method is adequate and gives less distortions;

hence, if future investigations are attempted, the methods will be used in the reverse order from that given above.

POSTSCRIPT.—Williams (1966) recently has described a new species, *Callinectes similis*, from eastern America that had been confused previously with *C. ornatus* and *C. danae*. Using the features listed in table 1, we find that the species appears, from the description, to resemble *C. danae* rather than *C. ornatus* in three features and to resemble *C. ornatus* rather than *C. danae* in two. The new species also differs from the other two in one listed feature, viz. *55*. The existence of another species further increases the "cohesion" of the genus and supports its claim for continued generic status.

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Specific and generic authors have been omitted for those American species dealt with in Rathbun (1930) or in Garth and Stephenson (1966), and for the Indo-West Pacific species dealt with in Stephenson, Hudson, and Campbell (1957) or in Stephenson and Campbell (1959, 1960).

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TABLE 1.—*Features used in distinguishing species* (designed to give positive or negative answers; initially intended to cover the western American species of *Portunus*; the list has been expanded to cover the species of *Callinectes*)

Body region	*Morphological features*	*Their arbitrary numbers*
Front and orbital region	Four frontal lobes or teeth	*1*
	Frontal processes rounded lobes, not pointed teeth	*2*
	Median frontal lobes more protruding than lateral	*3*
	Inner supraorbital angle subdivided (or almost) into two	*4*
	Inner supraorbital angle not acute	*5*
	Inner supraorbital sinus open	*6*
	Outer supraorbital sinus open	*7*
	Suborbital sinus open	*8*
Third maxilliped	Anteroexternal angle of merus not expanded	*9*
	Generally hairy	*10*
	Normally covered with pile of hairs	*11*
	Narrow	*12*
	Without tubercular elevations	*13*
	Postlateral junctions not spinous	*14*
Carapace	Protogastric areas with granular patches	*15*
	Mesogastric with broad granular ridge	*16*
	Central gastric patch joining meso- and metagastrics	*17*
	Metagastrics a pair of short ridges	*18*
	Epibranchial ridges well developed	*19*
	Anterolateral granular patches present	*20*
	Anterior mesobranchial area bearing "almost a ridge"	*21*
	Posterior mesobranchial ridge present	*22*
	Cardiac area with narrow, prominent, separate ridges	*23*
	Lateral postcardiac areas with granular patches	*24*
	Median postcardiac area with granular patches (often inconspicuous)	*25*
Anterolateral teeth	First stouter than second	*26*
	With a hint of being alternately large and small	*27*
	Last tooth distinctly long	*28*
Chelae	Not attenuated	*29*
	Robust, not slender	*30*
	Undersurface not smooth, tending to squamiform markings	*31*
	Posterior border of arm not with two spines	*32*
	Posterior border of arm not without spines	*33*
	Spine on inner surface wrist not particularly long	*34*
	Spine on inner surface wrist not reduced to tubercle	*35*
	Upper plus outer surface wrist with only one spine	*36*
	Hand not swollen	*37*
	Inner surface hand with carina	*38*
	Upper surface hand with one spine only	*39*
	Upper surface hand with spine on inside only	*40*
	Fingers strongly carinated	*41*
	Upper margin moveable finger not fringed with hairs	*42*
Fifth leg	Posterodistal border merus bearing spine or spines	*43*
	Border bearing spinules	*44*

TABLE 1.—Continued

Body region	*Morphological features*	*Their arbitrary numbers*
Male abdomen	Overall a moderately elongate triangle	*45*
	Penultimate segment with slightly sinuous sides	*46*
	Penultimate segment broad (1/b 1−1½)	*47*
	Ultimate segment lanceolate, not triangular with rounded tip	*48*
	Ultimate segment narrow (1/b >1)	*49*
First male pleopod	Smoothly curving, not sinuous	*50*
	Curving evenly throughout, distal portion not straight	*51*
	Not robust	*52*
	Not attenuated	*53*
	Without stout erect spines	*54*
	Outer surface subterminally with recurved spinules	*55*
	Inner surface subterminally with minute hairs or their follicles	*56*
General	No iridescence on body	*57*

TABLE 2.—*Data on material examined* (AHF=Allan Hancock Foundation, University of Southern California; SIO=Scripps Institute of Oceanography; USNM=United States National Museum; UQ=University of Queensland, Department of Zoology; entire collection examined unless indicated otherwise)

Species	*Number*	*Distribution*	*Specimens examined*
Portunus acuminatus (Stimpson) 1871	①	western America	AHF (including neotype)
P. angustus Rathbun 1898	②	Galapagos Islands	AHF, USNM (part, including holotype)
P. asper (A. Milne Edwards) 1861	③	western America	AHF, USNM (part)
P. brevimanus (Faxon) 1895	④	islands off western America	AHF, USNM (part, including holotype)
P. guaymasensis Garth and Stephenson 1966	⑤	Gulf of California	Holotype (unique)
P. iridescens (Rathbun) 1893	⑥	western America	AHF, USNM (part, including holotype)
P. stanfordi Rathbun 1898	⑦	Galapagos Islands	AHF, USNM (part, including holotype)
P. x. xantusii (Stimpson) 1860	⑧	western America	AHF, USNM (part)
P. x. affinis (Faxon) 1893	⑨	western America	AHF, USNM (part)
P. tuberculatus (Stimpson) 1860	⑩	western America	AHF, USNM (part, including cotype)
P. anceps (Saussure) 1858	⑪	eastern America	AHF (part) and USNM (part)
P. bahamensis Rathbun 1930	⑫	eastern America	USNM (part, including types)
P. depressifrons (Stimpson) 1859	⑬	eastern America	AHF (part), USNM (part)
P. floridanus Rathbun 1930	⑭	eastern America	AHF (part), USNM (types)
P. gibbesii (Stimpson) 1859	⑮	eastern America	USNM (part)
P. ordwayi (Stimpson) 1860	⑯	eastern America	AHF, USNM (part)

TABLE 2.—Continued

Species	Number	Distribution	Specimens examined
P. rufiremus Holthuis 1959	⑰	eastern America	USNM (paratypes)
P. sayi (Gibbes) 1850	⑱	eastern America, southern Indian Ocean	USNM (part)
P. sebae (H. Milne Edwards) 1834	⑲	eastern America	USNM (part)
P. spinicarpus (Stimpson) 1871	⑳	eastern America	USNM (part)
P. spinimanus Latreille 1819	㉑	eastern America	USNM (part)
P. ventralis (A. Milne Edwards) 1879	㉒	eastern America	USNM (part)
P. vocans (A. Milne Edwards) 1878	㊸	eastern America, western Africa	USNM (?part)
P. macrophthalmus Rathbun 1906	㉓	Indo-West Pacific	USNM (holotype)
P. pelagicus (Linnaeus) 1766	㉔	Indo-West Pacific, Mediterranean	USNM (part), SIO, UQ (part)
P. pubescens (Dana) 1852	㉕	Indo-West Pacific	USNM (part)
P. sanguinolentus (Herbst) 1796	㉖	Indo-West Pacific, Mediterranean	UQ (part)
P. convexus de Haan 1833	㊹	Indian Ocean	(literature only)
P. cf. *trituberculatus* (Miers) 1876	㊺	Indo-West Pacific	UQ (single specimen)
Callinectes arcuatus Ordway 1863	㉗	western America	AHF, USNM (part)
C. bellicosus (Stimpson) 1859	㉘	western America	AHF, USNM (part)
C. boucourti A. Milne Edwards 1879	㉙	eastern America	USNM (part)
C. danae Smith 1869	㉚	eastern America	USNM (part)
C. exasperatus (Gerstaecker) 1856	㉛	eastern America	USNM (part)
C. gladiator Benedict 1893	㉜	western Africa	USNM (part)
C. latimanus Rathbun 1897	㉝	western Africa	USNM (part, including type)
C. marginatus (A. Milne Edwards) 1861	㉞	eastern America, western Africa	USNM (part)
C. ornatus Ordway 1863	㉟	eastern America	USNM (part)
C. sapidus Rathbun 1895	㊱	eastern America	USNM (part)
C. s. acutidens Rathbun 1895	㊲	eastern America	USNM (part, including cotype)
C. tozotes Ordway 1863	㊳	western America	AHF, USNM
Arenaeus cribrarius (Lamarck) 1818	㊴	eastern America	AHF, USNM (part)
A. mexicanus (Gerstaecker) 1856	㊵	western America	AHF, USNM (part)
Scylla serrata (Forskål) 1753	㊶	Indo-West Pacific	USNM (part), SIO, UQ (part)

TABLE 3.—*Agreements(+)and disagreements(−)of species to features in table 1* (doubtful cases ringed; ?=doubtful feature from literature)

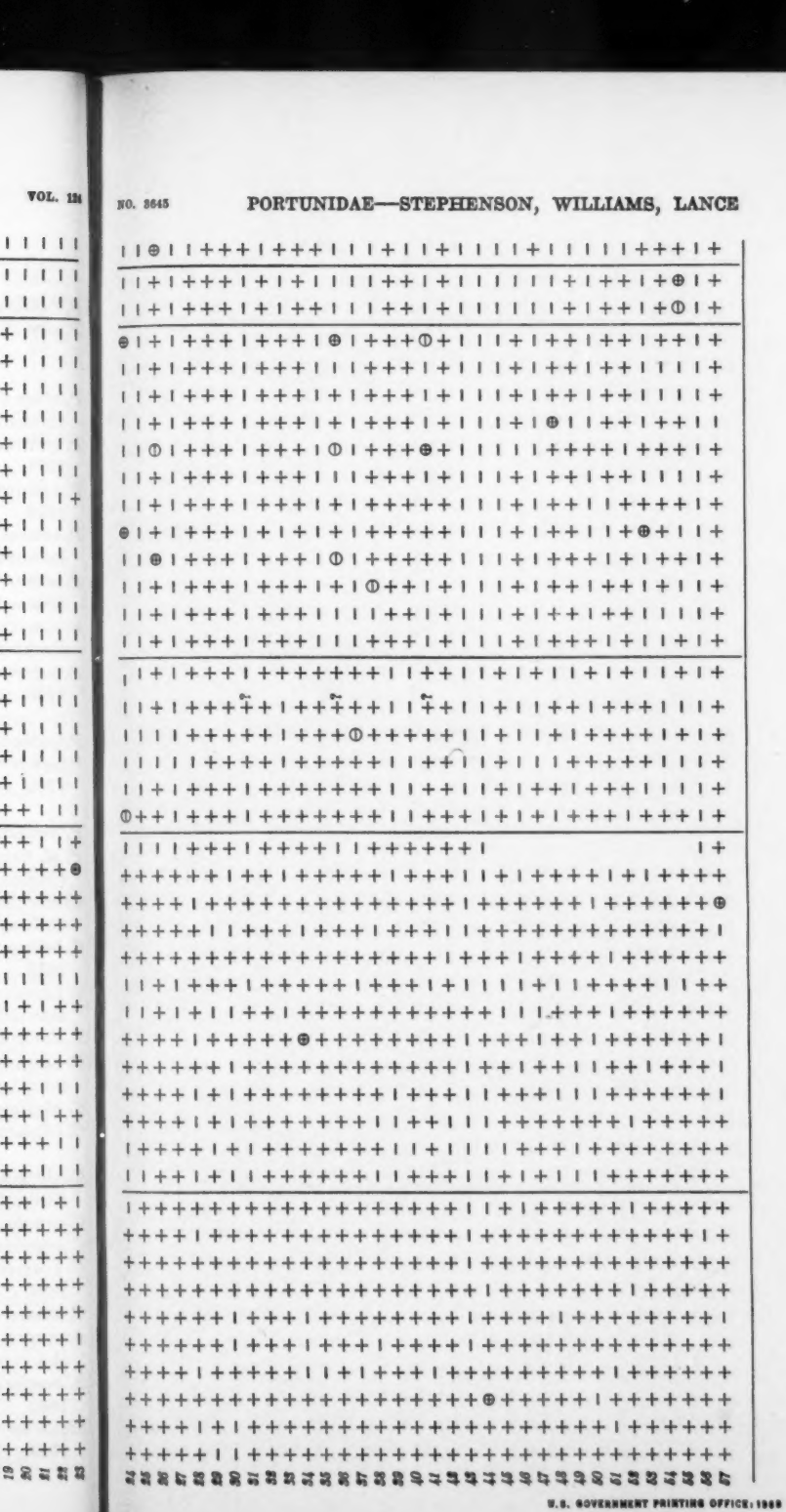
			① accumbatus	+ +
			② angulatus	+ +
			③ asper	+ +
			④ brevimanus	+ +
			⑤ quagmaensis	+ +
			⑥ trilaceras	+ +
			⑦ alanjordi	+ +
			⑧ x. zanluelli	+ +
			⑨ x. affinis	+ +
			⑩ tuberculatus	+ +
			⑪ anceps	+ +
			⑫ balanarcalis	+ +
			⑬ depressifrons	+ +
			⑭ floridanus	+ +
			⑮ gibbarii	+ +
			⑯ ordwayi	+ +
			⑰ rufirenus	+ +
			⑱ sayi	+ +
			⑲ sebae	+ +
			⑳ sphincterpus	+ +
			㉑ sphinctinanus	+ +
			㉒ ventralis	+ +
			㉓ socanus	+ +
			㉔ macrophthalmus	+ +
			㉕ pelagicus	+ +
			㉖ pulcherrimus	+ +
			㉗ sanguinolentus	+ +
			㉘ socotranus	+ +
			㉙ cf. tribuberculatus	+ +
			㉚ arcuatus	+ +
			㉛ ballicornis	+ +
			㉜ boucourti	+ +
			㉝ danae	+ +
			㉞ exasperatus	+ +
			㉟ floridanus	+ +
			㊱ lafitteri	+ +
			㊲ marginatus	+ +
			㊳ ornatus	+ +
			㊴ sayi	+ +
			㊵ s. occidens	+ +
			㊶ torcoa	+ +
			㊷ cribraria	+ +
			㊸ mexicanus	+ +
			㊹ arenata	+ +
				1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

Portunus — western American; eastern American; Indo-West Pacific

Callinectes

Arenaeus

Scylla



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